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Far-red Light in Sole-source Lighting Can Enhance the Growth and Fruit Production of Indoor Strawberries

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Abstract. **Strawberries (*Fragaria ×ananassa*) are being produced increasingly in indoor vertical farms, where the light quality of sole-source lighting is a primary factor that influences the outcomes of crop production. Far-red (FR) light (700–750 nm) has been shown to promote plant responses such as leaf expansion, biomass accumulation, and flowering in some long-day plant species. However, the impacts of including FR light in sole-source lighting on strawberries have not been fully understood. This study investigated the impacts of FR light on the growth and development of long-day strawberries 'Albion' and 'Monterey' in an indoor vertical farm. We hypothesized that the addition of FR light under a long photoperiod would promote leaf expansion, biomass accumulation, flowering, and fruit production in long-day strawberries. Bare-root strawberry plants were grown in a deep-water-culture hydroponic system at an air temperature of 22 °C and an 18-hour photoperiod using 90 μmol·m^{-2}·s^{-1} of blue (peak = 455 nm) + 250 μmol·m^{-2}·s^{-1} of red (peak = 660 nm) light-emitting diodes (LEDs) with or without adding 50 μmol·m^{-2}·s^{-1} of FR (peak = 730 nm) LEDs. After 5 weeks of lighting treatments, additional FR light increased the leaf area and shoot dry mass of strawberry 'Monterey' by 74% and 73%, respectively, and the number of crowns per plant of strawberry 'Albion' by 33%. However, FR light did not influence flowering time in either cultivar. Adding FR light increased the number of fruit harvested per plant by 36%, the total fruit yield by 48%, and the total soluble solids of fruit by 12% in strawberry 'Albion', but not in 'Monterey'. In both cultivars, FR light did not affect the individual fruit mass. Our results suggest that the addition of FR light in sole-source lighting can promote leaf expansion, biomass accumulation, fruit yield, and fruit quality in at least some long-day strawberry cultivars.**

Strawberries (*Fragaria ×ananassa*) are a highly valued specialty food crop, valued at more than $3.1 billion in 2022 in the United States (US Department of Agriculture, National Agricultural Statistics Service 2022). However, outdoor growers are facing an increasing number of challenges, including more variable weather conditions, a decreasing labor supply, tightening environmental regulations, and increases in land value (Samtani et al. 2019). In response, cultivating strawberry crops in indoor vertical farms is increasingly appealing. With proper cultural practices, strawberry crops can remain compact and respond well to hydroponic growing conditions and indoor growing environments, making them suitable for production in indoor vertical farms (Richardson et al. 2022). As a result, many established and startup indoor vertical farming companies are beginning to produce strawberries at a commercial level (Lore 2022; Marston 2023).

Because crop production in indoor vertical farming is highly energy intensive and costly, it is critical to optimize the environmental conditions to improve crop productivity and quality (Bantis et al. 2018). In indoor vertical farms, the sole-source lighting strategy applied is among the most important environmental factors that affect crop yield and productivity. Sole-source lighting supplies light completely artificially, typically using light-emitting diodes (LEDs), which allow growers to deliver unique combinations of light wavebands for each specific crop. Given that light quality can affect a wide range of plant traits, such as plant height, leaf size, and flowering time, and that these responses can vary across plant species and cultivars (Rahman et al. 2021), determining the optimal light spectrum specifically for strawberries is crucial for their effective production in indoor vertical farms.

In strawberries, light quality studies in sole-source lighting have focused primarily on blue (B) light (400–500 nm) and red (R) light (600–700 nm). Monochromatic B light can improve the vegetative, flowering, and fruiting stages of strawberries compared with monochromatic R light. For example, monochromatic B light (peak = 436 nm) increased petiole length, flower stem length, fruit set, and fruit yield, and accelerated flowering compared with monochromatic R light (peak = 666 nm) in strawberry 'Elsanta' (Nadalini et al. 2017). The time to flower initiation was reduced by 17 d using B light (peak = 470 nm) over R light (peak = 630 nm) in long-day strawberry 'HS138' (Yoshida et al. 2012). However, different combinations of B + R lighting have enhanced growth and fruiting parameters compared with B or R light alone. For example, B + R LED light produced the greatest yield in 'Daewang' strawberries compared with B light (peak = 448 nm) or R light (peaks = 634 nm and 661 nm) alone in a growth chamber, and a greater sucrose content was produced using B + R light compared with B light alone (Choi et al. 2015). In addition, a combination of B + R light increased the total chlorophyll content compared B or R light individually (Choi et al. 2015). Combining with R light (peak = 640) with B light (peak = 455) improved vegetative growth and increased individual fruit fresh mass in strawberry 'Elkat' compared with R light (peak = 640 nm) only in a phytotron chamber (Samuolienė et al. 2010). In strawberry 'Daewang', a combination of B and R light increased overall fruit yield and fructose content over monochromatic B light (peak = 448 nm) or R light (peak = 661 nm).

Recently, including far-red (FR) light (700–750 nm) in sole-source lighting has received attention because of its positive effects on photosynthesis and photomorphogenesis (Tan et al. 2022). Although the traditionally defined range of photosynthetically active radiation (PAR; 400–700 nm) excludes FR light, FR light elicits comparable photosynthetic activity when combined with PAR photons (Zhen and van Iersel 2017; Zhen et al. 2021). On the other hand, FR light influences plant development through phytochromes, which are photoreceptor proteins present in plants. Phytochromes exist in two forms: Pr (inactive) and Pfr (active). The absorption of R light causes a structural change in the phytochrome molecule, converting the Pr form to the Pfr form, the relative proportions of which can determine plant physiological processes such as stem elongation, leaf expansion, and, in some cases, flowering. The balance of Pfr to Pr can be estimated by measuring the spectral distribution of photons received by plants and by using photoconversion coefficients to obtain a value that represents the ratio of Pfr to (Pr + Pfr), known as the phytochrome photoequilibria (PPE) (Sager et al. 1988). An improvement to this calculation has been suggested by Kusuma and Bugbee (2021), which incorporates the

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scattering and absorbance of photons within leaves to predict phytochrome responses more effectively, known as internal PPE (iPPE). In tomato (*Solanum lycopersicum*), adding FR light to B + R light increased plant height, leaf area, and plant dry mass over plants receiving B + R light only (Kalaitzoglou et al. 2019). The promotive effects of including FR in sole-source lighting on stem elongation, leaf expansion, and biomass accumulation have also been observed in many horticultural crops, including geranium (*Pelargonium ×hortorum*), petunia (*Petunia ×atkinsiana*), snapdragon (*Antirrhinum majus*), impatiens (*Impatiens walleriana*), marigold (*Tagetes erecta*), zinnia (*Zinnia elegans*), dianthus (*Dianthus barbatus ×chinensis*), sunflower (*Helianthus annuus*), lettuce (*Lactuca sativa*), and cucumber (*Cucumis sativus*) (Kurepin et al. 2007; Kusuma and Bugbee 2023; Park and Runkle 2017; Zhen and Bugbee 2020). Furthermore, in long-day (LD) plants snapdragon and petunia, adding $\geq$ 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light in sole-source lighting has been shown to accelerate flowering (Park and Runkle 2017, 2018; Zhang et al. 2020).

The inclusion of FR light has shown promotive effects on flowering in some LD strawberry cultivars and accessions. For example, an LD strawberry accession (*Fragaria vesca* 'Hawaii-4') flowered a month earlier under end-of-day lighting from FR LEDs or incandescent lamps, which also emit FR light, than under R light (Rantanen et al. 2014). Similarly, flower induction was promoted in an LD strawberry accession, *F. vesca* 'Yellow Wonder', by supplying FR light (peak = 740 nm) for 24 h (Prisca et al. 2022). Flower bud emergence was accelerated in seedlings of LD strawberry cultivars Elan and Yotsuboshi by adding FR light (peak = 730 nm) to B (peak = 470 nm) + R (peak = 625 nm) light for 24 h (Tsuruyama and Shibuya 2023). Collectively, the promotive effects of FR light on flowering in some LD plants are applicable to at least some LD or long-day strawberries. However, previous strawberry studies focused on flowering responses to FR light, with a lack of emphasis on analyzing vegetative growth, and fruit yield and quality. The objective of our study was to investigate the effects of including FR light in sole-source lighting on plant morphology, biomass accumulation, flowering, and subsequent fruit yield and quality in long-day strawberries. We postulated that additional FR light would promote leaf expansion, biomass accumulation, and flowering, thereby increasing fruit yield and quality in long-day strawberries.

Materials and Methods

Plant materials and transplanting. We obtained bare-root plants of two long-day strawberry cultivars, Albion and Monterey, from a commercial nursery (Lassen Canyon Nursery Inc., Redding, CA, USA) on 24 Aug 2022. For each cultivar, we selected 100 bare-root plants with crown diameters of 10 to 13 mm for experimental use on 26 Aug 2022. Average crown diameters of the bare-root plants for 'Albion' and 'Monterey' were 11.2 mm and 11.3 mm, respectively. We washed the bare-root plants with tap water to remove residual media and sanitized them in a solution made with Zerotol (27.1% hydrogen peroxide and 2.0% peroxyacetic acid; Biosafe Systems, East Hartford, CT, USA) and deionized water (1:100 $mL \cdot mL^{-1}$) for 15 min.

We then moved the plants to a temperature-controlled indoor vertical farm and transplanted them into foam rafts (28-cell lettuce raft; Beaver Plastics Ltd., Acheson, Alberta, Canada) floating in deep-water-culture hydroponic growing trays (1.12 × 0.66 × 0.18 m; GT24X44X7B; Botanicare, Vancouver, WA, USA). Four growing racks were used, each of which contained three vertically stacked tiers that held a growing tray in each tier, totaling 12 growing trays. At the bottom of each rack there were two reservoirs with recirculating water (0.80 × 0.53 × 0.37 m; 94 Liter Latch and Stack Tote; Husky, Atlanta, GA, USA), which connected to the growing trays. Each foam raft (growing area, 0.74 m^2) held 25 plants (planting density, 27 plants/m^2), which were of the same cultivar in each tier, and the cultivars were arranged identically between replications and treatments on each rack. The experiment was carried out using a randomized complete block design, with each replication as a block, each reservoir as the experimental unit for the lighting treatment, and the individual plant of each cultivar as a subsample. The vertical location of each floating raft in the growing rack was cycled every 2 weeks for the duration of the experiment to reduce any positional effects in the growing trays in the growing rack, with the top raft moved to the bottom, the bottom raft moved to the middle, and the middle raft moved to the top.

Air temperature was maintained at 22 °C and logged on an hourly basis with a sensor placed in the center of each growing tray (Smart Thermo-Hygrometer H5075; Govee, Shenzen, China). A nutrient solution made with deionized water and the Yamazaki recipe provided 77 $mg \cdot L^{-1}$ N, 23 $mg \cdot L^{-1}$ P, 116 $mg \cdot L^{-1}$ K, 48 $mg \cdot L^{-1}$ S, 40 $mg \cdot L^{-1}$ Ca, 12 $mg \cdot L^{-1}$ Mg, 2 $mg \cdot L^{-1}$ Fe, 0.6 $mg \cdot L^{-1}$ Mn and Zn, 0.3 $mg \cdot L^{-1}$ B, 0.05 $mg \cdot L^{-1}$ Cu, and 0.01 $mg \cdot L^{-1}$ Mo (Jack's Strawberry Part A/B; JR Peters, Inc., Allentown, PA, USA) for the entire growing period. The nutrient solution within each rack was circulated continuously with water pumps (396 GPH Fixed Flow Water Pump; Sunlight Supply Vancouver, WA, USA) and oxygenated with an air pump (Vivosun Electrical Magnetic Air Pump ACO-050; Ontario, CA, USA) and air stones (ASD-200; Pawfly Guangzhou City, Guangdong, China). Daily measurements of the nutrient solution pH and electrical conductivity (EC) were taken with a portable meter (HI9814; Hanna Instruments, Smithfield, RI, USA), and the pH was adjusted to 5.8 if outside 5.5 to 6.0, using 50% sulfuric acid to lower the pH and potassium bicarbonate to increase the pH, whereas EC was kept to less than 2.0 $mS \cdot cm^{-1}$ by adding deionized water.

Lighting treatments. After transplanting, the bare-root plants were grown under B (peak = 455 nm) + R (peak = 660 nm) or B (peak = 455 nm) + R (peak = 660 nm) + FR (peak = 730 nm) LED lamps (T8 Double-Row LED Indoor Grow Light; Homer Farms, Inc., Mesa, AZ, USA) (Fig. 1; Table 1) as sole-source lighting treatments with an 18-h photoperiod. Each growing tray had seven or eight LED lamps for B + R or B + R + FR

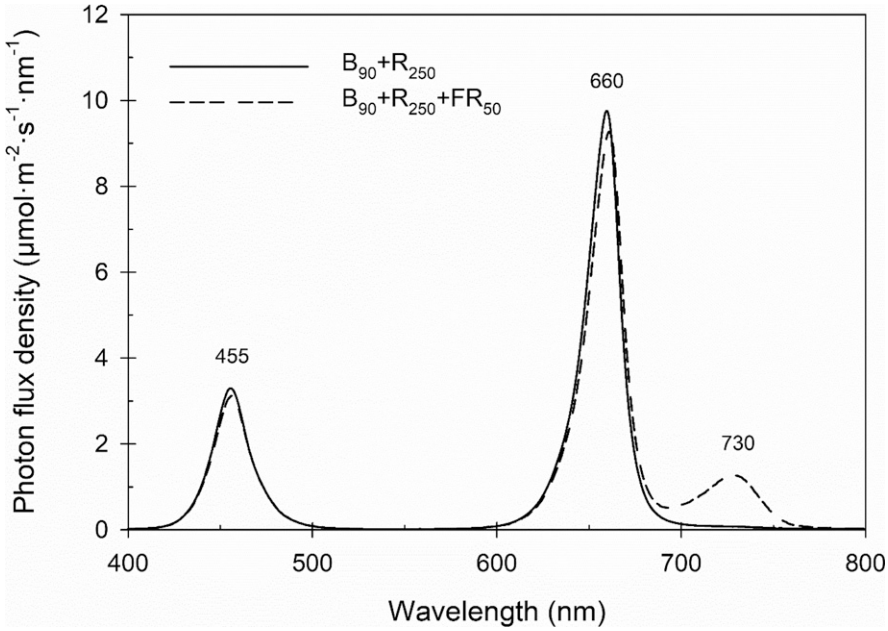

Fig. 1. The spectral distribution of the blue + red (B_{90} + R_{250}) and blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diodes (LEDs) used in the sole-source lighting treatments. The number after each LED type is its photon flux density. The numbers above the spectral distribution curves represent the peak wavelengths.

Table 1. Spectral characteristics of the blue + red (B_{90} + R_{250}) and blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diodes used in the sole-source lighting treatments.

Lighting treatment[i]	PPFD, 400–700 nm ($\mu mol \cdot m^{-2} \cdot s^{-1}$)[ii]	ePPFD, 400–750 nm ($\mu mol \cdot m^{-2} \cdot s^{-1}$)[iii]	FR (%)[iv]	PPE[v]	iPPE[vi]
B_{90} + R_{250}	345.7	349.0	0.9	0.876	0.846
B_{90} + R_{250} + FR_{50}	338.5	388.0	11.9	0.841	0.660

[i] B = blue; R = red. The number after each light-emitting diode type is its photon flux density measured in micromoles per square meter per second.
[ii] PPFD = photosynthetic photon flux density.
[iii] ePPFD = extended photosynthetic photon flux density.
[iv] FR = far red. The percentage of FR (700–750 nm) photon flux density relative to ePPFD.
[v] PPE = phytochrome photoequilibria. The estimated P_{FR}/P_{R+FR}, where P is phytochrome, according to Sager et al. (1988).
[vi] iPPE = internal phytochrome photoequilibria. The estimated P_{FR}/P_{R+FR} within a leaf, according to Kusuma and Bugbee (2021).

treatments, respectively, positioned 25.5 cm above the growing area. At plant height, the B + R treatment delivered 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light and 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light, whereas the B + R + FR treatment delivered 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light, 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light, and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light. Photon flux densities were measured using a spectroradiometer (PS-300; StellerNet, Inc., Tampa, FL, USA) at nine equally spaced locations in each growing tray at plant height (Fig. 1). With the spectra in Fig. 1, the percentage of FR light was calculated as the percentage of the photon flux density of FR light (700–750 nm) in the extended photosynthetic photon flux density (ePPFD) (400–750 nm), PPE was calculated as described in Sager et al. (1988), and the estimated iPPE was calculated according to Kusuma and Bugbee (2021) (Table 1). Photon flux densities of $\geq$ 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and an 18-h photoperiod were chosen based on a previous finding (Park et al. 2023) that a longer photoperiod at a photosynthetic photon flux density (PPFD) of $\geq$ 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ promoted flowering and fruit yield.

Data collection and analysis. The experiment was replicated in independent growing racks during the same experimental period. In each replication, during the initial 5-week period after transplanting, all flowers and runners were removed daily to promote vegetative growth. Five weeks after transplanting, 10 representative plants of each cultivar, treatment, and replication were chosen randomly for vegetative growth data collection. At the time of collecting vegetative growth data, each plant was not in contact with another (leaf area index, < 1). For each plant, we recorded the number of fully formed trifoliate leaves, soil plant analysis development (SPAD) index [using a portable chlorophyll meter (SPAD-502; Konica Minolta Sensing, Inc., Chiyoda, Tokyo, Japan)], crown number, crown diameter [using a caliper (B07DFFYCXS; Adoric)], leaf area [using a leaf area meter (LI-3100; LI-COR Inc., Lincoln, NE, USA)], root length, and shoot and root fresh and dry mass [using a scale (PB602-S; Mettler Toledo, Columbus, OH, USA)]. Shoot and root dry mass were measured after plants were dried sufficiently at $\geq$ 70 °C for $\geq$ 5 d in a drying oven (Hafo 1600; VWR International, LLC, Aurora, CO, USA).

Following vegetative growth data collection, each plant was allowed to develop flowers and fruit. For each plant, we recorded the date of the first open flower and the date of the first fruit harvest (at the visual appearance of the first fully red fruit). Fruit harvesting started 66 d after transplanting, with subsequent fruit data collected for all ripened fruit twice weekly for the remainder of the experiment. In addition, 11 weeks after transplanting, the numbers of unopened flowers, fully opened flowers, fruit, and inflorescences were counted for all remaining plants, and the length of the peduncles for inflorescences was determined for harvestable fruit. After each fruit was harvested, we measured the fruit diameter at its largest width and vertical length using a caliper (B07DFFYCXS; Adoric), and fruit fresh mass was determined using an analytical balance (PB602-S; Mettler Toledo). For each plant, we measured the total soluble solids (TSS), reported in degrees Brix, of the first harvested fruit at room temperature. The largest fruit was chosen if the plant had multiple harvestable fruit. After a fruit was selected for TSS measurement, we removed its pedicle and placed it in a plastic bag, where it was compressed by hand until it reached a consistent pulp state. A TSS reading was then taken using a digital refractometer (HI 96801; Hanna Instruments), which also recorded ambient temperature.

Data were analyzed using Student's *t* test in SAS v. 9.4 (SAS Institute, Inc., Cary, NC, USA) using PROC TTEST, with a significance level at $P < 0.05$. The experiment was replicated, and data from each replication were pooled for the *t* test because the experimental conditions remained consistent across replications, each replication was conducted independently, lighting treatments were assigned randomly within each replication, and pooling data from multiple replications can enhance the power of the analysis. The sample sizes for the analysis of vegetative growth (n = 20), days to flower and fruit harvest (n = 24), peduncle length (n = 16), and fruit production and characteristics (n = 24) varied.

Results

Vegetative growth. The addition of FR light increased the number of crowns in 'Albion' by 33%, but not in 'Monterey' (Table 2). Leaf number, crown diameter, and SPAD index for both 'Albion' and 'Monterey' were unaffected by FR light. In 'Monterey', additional FR light increased leaf area by 74%, shoot fresh mass by 59%, and shoot dry mass by 73%, whereas FR light did not influence these parameters in 'Albion'. In 'Monterey', FR light also increased root fresh mass by 62%, root dry mass by 47%, and root length by 17%; however, root growth of 'Albion' was unaffected by FR light.

Table 2. Growth characteristics of strawberry 'Albion' and 'Monterey' plants grown for 5 weeks under blue + red (B_{90} + R_{250}) or blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diode lighting treatments.

Lighting treatment[i]	Leaf no.	Leaf area (cm^2)	SPAD index[ii]	Crown no.	Crown diam (mm)	Shoot fresh mass (g)	Root fresh mass (g)	Shoot dry mass (g)	Root dry mass (g)	Root length (cm)
Albion										
B_{90} + R_{250}	3.6	237.2	46.4	1.5 a[iii]	11.8	18.1	24.9	4.0	1.9	27.3
B_{90} + R_{250} + FR_{50}	3.7	242.8	45.3	2.0 b	12.2	18.7	23.4	4.3	1.9	27.2
Significance	NS[iv]	NS	NS	*	NS	NS	NS	NS	NS	NS
Monterey										
B_{90} + R_{250}	3.2	120.1 a	41.1	1.8	11.6	10.8 a	14.6 a	2.1 a	1.3 a	26.0 a
B_{90} + R_{250} + FR_{50}	4.0	209.2 b	39.9	2.1	11.6	17.3 b	23.6 b	3.6 b	1.9 b	30.4 b
Significance	NS	**	NS	NS	NS	**	**	**	**	**

[i] B = blue; R = red. The number after each light-emitting diode type is its photon flux density measured in micromoles per square meter per second. Data represent the mean of two replications, with 10 plants per replication (n = 20).
[ii] SPAD = soil plant analysis development.
[iii] Means followed by different letters within columns for each cultivar are significantly different by *t* test at $P < 0.05$.
[iv] NS, *, **Nonsignificant or significant at $P < 0.05$ or 0.01, respectively.

Table 3. Days to flower and fruit harvest (after transplanting) of strawberry 'Albion' and 'Monterey' plants grown under blue + red (B_{90} + R_{250}) or blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diode lighting treatments.

Cultivar and treatment[i]	Days to flower	Days to fruit harvest
Albion		
B_{90} + R_{250}	50	79 a[ii]
B_{90} + R_{250} + FR_{50}	51	74 b
Significance	NS[iii]	**
Monterey		
B_{90} + R_{250}	49	77
B_{90} + R_{250} + FR_{50}	49	74
Significance	NS	NS

[i] The number after each light-emitting diode type is its photon flux density measured in micromoles per square meter per second. Data represent the mean of two replications, with 12 plants per replication (n = 24).

[ii] Means followed by different letters within columns for each cultivar are significantly different by *t* test at $P < 0.05$.

[iii] NS, **Nonsignificant or significant at $P < 0.01$, respectively.

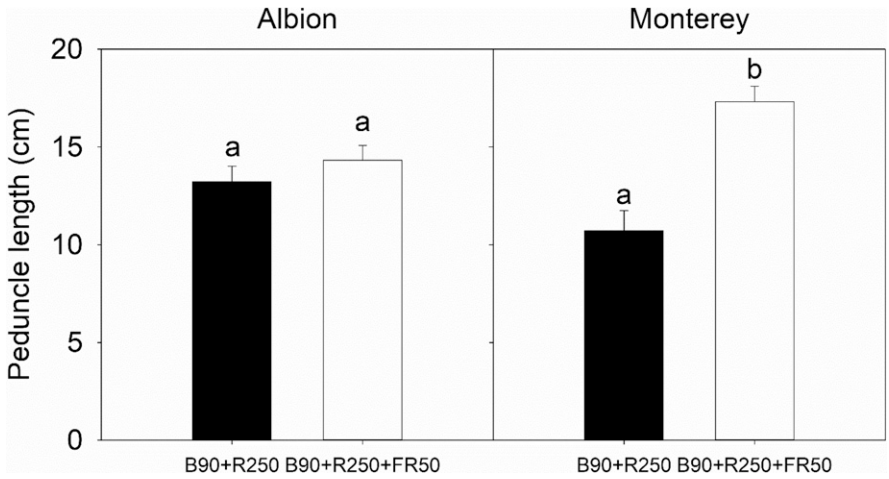

Fig. 2. Peduncle length of strawberry 'Albion' and 'Monterey' plants with ripened fruit grown under blue + red (B_{90} + R_{250}) or blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diode (LED) lighting treatments. The number after each LED type is its photon flux density measured in micromoles per square meter per second. Data represent the mean and standard error of two replications, with eight plants per replication (n = 16). Means followed by different letters for each cultivar indicate statistically significant differences between lighting treatments at $P < 0.05$.

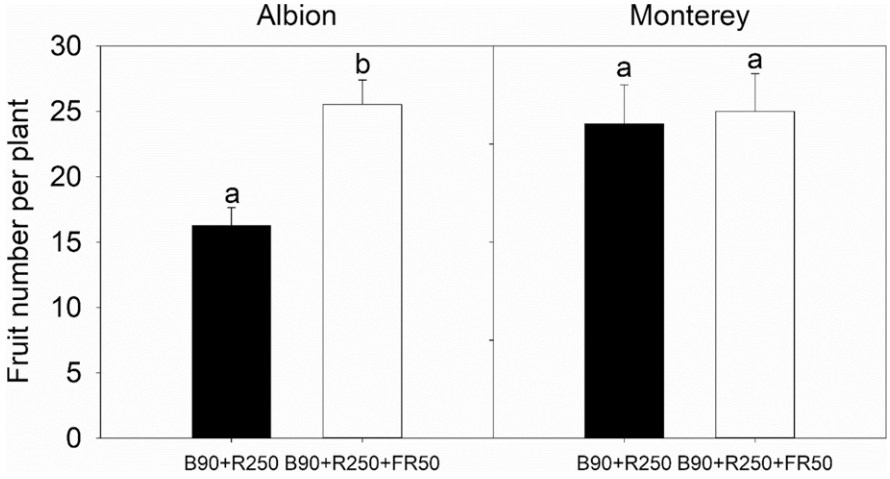

Fig. 3. Number of fruit produced per plant of strawberry 'Albion' and 'Monterey' grown under blue + red (B_{90} + R_{250}) or blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diode (LED) lighting treatments. The number after each LED type is its photon flux density measured in micromoles per square meter per second. Data represent the mean and standard error of two replications, with 12 plants per replication (n = 24). Means followed by different letters for each cultivar indicate statistically significant differences between lighting treatments at $P < 0.05$.

Flowering and fruit production. FR light had little to no effect on days to flowering in both cultivars and days to fruit harvest in 'Monterey' (Table 3). In 'Albion', FR light hastened fruit harvest by 5 d. At fruit harvest, FR light increased the peduncle length by 62% in 'Monterey', but not in 'Albion' (Fig. 2). FR light increased the number of fruit and total fruit fresh mass produced per plant by 36% and by 48%, respectively, in 'Albion', but not in 'Monterey' (Figs. 3 and 4). Individual fruit produced in both cultivars had similar fresh mass and fruit length regardless of FR light; however, FR light decreased the fruit diameter by 3% to 4% (Table 4). FR light increased the TSS value of 'Albion' fruit by 12% but did not influence that of 'Monterey' fruits.

Discussion

In our study, when 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light (or decreasing PPE from 0.88 to 0.84) was added to 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light + 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light, both shoot dry mass and leaf area of strawberry 'Monterey' increased by 73% and 74%, respectively, showing a similar magnitude of change. Adding FR light to sole-source lighting promotes leaf expansion and biomass accumulation of many horticultural crops, such as lettuce, petunia, and geranium (Park and Runkle 2017, 2018, 2019; Kusuma and Bugbee 2023). In addition, because leaf expansion contributes significantly to the rate of biomass accumulation, the increase in shoot dry mass was comparable to the increase in leaf area with the addition of FR light. For example, in lettuce, adding 52 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to 24 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light and 194 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light increased leaf area by 61% and leaf dry mass by 63% (Jin et al. 2021). In *Crepidiastrum denticulatum*, adding 108.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to 32.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light and 97.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light (decreasing PPE from 0.88 to 0.71) increased shoot dry mass by 90% and leaf area by 96% (Bae et al. 2017).

The extent of the increase in leaf area and shoot dry mass observed in 'Monterey' (73% and 74%, respectively) is greater than what has been reported in other shade-avoiding horticultural crops receiving FR light, given the relatively small amount of an additional percentage of FR light supplied here (12% FR). For example, adding 40% FR light increased the leaf area and shoot dry mass of petunia by 65% and 50%, respectively (Park and Runkle 2018). In geranium, adding 10% FR light led to a 2% increase in leaf area and a 17% increase in shoot dry mass (Park and Runkle 2017). Similarly, a 6% FR light addition in geranium increased leaf area and shoot dry mass by 6% and 16%, respectively (Park and Runkle 2019). Leaf length was increased by 33% and shoot dry mass by 47% in lettuce 'Rouxai' with a 17% FR addition (Meng and Runkle 2019). Considering that plants may display varying sensitivity to FR light depending on whether they exhibit shade-avoiding or shade-tolerant traits (Roig-Villanova and Martínez-García 2016), the increases in leaf

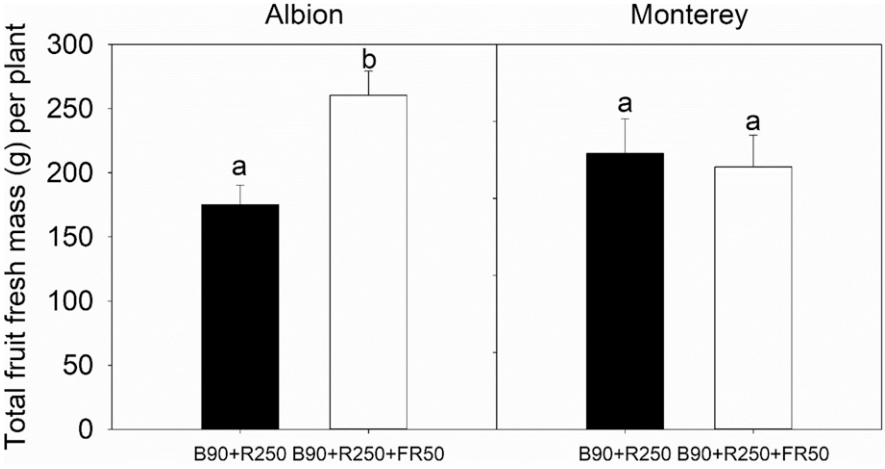

Fig. 4. Total fresh mass of fruit produced per plant of strawberry 'Albion' and 'Monterey' grown under blue + red (B_{90} + R_{250}) or blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diode (LED) lighting treatments. The number after each LED type is its photon flux density measured in micromoles per square meter per second. Data represent the mean and standard error of two replications with 12 plants per replication (n = 24). Means followed by different letters for each cultivar indicate statistically significant differences between lighting treatments at $P < 0.05$.

area and shoot dry mass observed in strawberries in our study indicate a high sensitivity to FR light in certain strawberry cultivars during the vegetative stage.

In contrast to 'Monterey', FR light did not affect leaf expansion or biomass accumulation in strawberry 'Albion'. Leaf expansion responses to FR light may depend on the overall ePPFD supplied and crop species (Kusuma and Bugbee 2023). For example, in lettuce, increasing the percentage of FR light promoted leaf expansion only under an ePPFD of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but not 100 or 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Kusuma and Bugbee 2023). Comparing the effects of R-to-FR ratios of 0.8, 1.4, and 4.5 at a low PPFD (157 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and a high PPFD (421 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in sunflower, increased leaf expansion by lowering the R-to-FR (or adding FR light) was more pronounced at the higher PPFD than at the lower PPFD (Kurepin et al. 2007). Hidaka et al. (2013) found that the photosynthetic rate of strawberries increased by increasing the PPFD up to 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, at which point the response was nearly saturated, and Park et al. (2023) observed a linear increase in shoot dry mass through increasing the PPFD from 200 to 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Considering the high light requirement for strawberries (Hidaka et al. 2013; Park et al. 2023), the ePPFD of 390 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in our study might not have been sufficiently high to induce fully the pronounced effects of FR light on promoting leaf expansion and dry mass accumulation in some strawberry cultivars.

In many LD plants, adding FR light to R light to elicit an intermediate PPE promotes flowering. For example, with a 4-h night interruption, R + FR light at an intermediate PPE (0.63–0.80) was most effective at inducing the flowering of snapdragon and petunia compared with a PPE of 0.46 or 0.16 (Craig and Runkle 2016). Under sole-source lighting conditions, adding ≥ 16 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to B + R light (PPE = 0.65–0.85) during an 18-h photoperiod decreased flowering time in snapdragon and petunia (Park and Runkle 2017, 2018, 2019; Zhang et al. 2020). Similarly, in the LD strawberry 'Elan', adding 63 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light (PPE = 0.66) to the background of B + R light during 16 or 24 h of sole-source lighting decreased the number of days to budding when compared with conditions solely under B + R light (PPE = 0.88) (Tsuruyama and Shibuya 2023). In our study, adding 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ FR light to the B + R light background decreased PPE from 0.88 to 0.84, making the PPE levels aligned within the range that has been reported previously as effective for stimulating flower initiation in some LD plants (Park and Runkle 2017, 2018, 2019; Zhang et al. 2020). However, the time to flowering was not affected by the addition of FR light or intermediate PPE in either cultivar in our study. In addition to FR light, B light can also regulate photoperiodic flowering responses in some LD plants (Lopez et al. 2020; Meng and Runkle 2017). For example, in calibrachoa (*Calibrachoa ×hybrida*), petunia, and snapdragon, 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light as night interruption was as effective for promoting flowering as end-of-day or night-interrupting treatments providing 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of combined R + W + FR light (Meng and Runkle 2017). In LD strawberry accession *F. vesca* 'Hawaii-4', 6 h of day-extending lighting with 7 to 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light promoted flowering over 12-h short-day or 6-h day-extending lighting with 7 to 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R light (Rantanen et al. 2014). In addition, flowering responses in some LD plants were saturated when day-extending or night-interrupting lighting included ≥ 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light (Lopez et al. 2020). Given the involvement of B light in photoperiodic flowering in LD plants and the observed saturation of B light-mediated photoperiodic flowering responses at a relatively low photon flux density, the application of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light for an 18-h photoperiod in both treatments in our study may have exceeded the threshold necessary to induce a flowering response in the long-day strawberry cultivars Monterey and Albion, mitigating any potential effects from FR light.

In this study, the addition of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ FR light (or adding 12% FR light) resulted in a 62% increase in peduncle length in strawberry 'Monterey'. Peduncles are specialized stems that can support either flowers or inflorescences in flowering plants or fruit in many fruiting crops. The promotive effects of FR light on the extension growth of peduncles were reported in other flowering crops. For instance, 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of localized FR radiation to peduncles increased the peduncle length of geranium (*Pelargonium zonale*) by 30% compared with B or R light at the same intensity (Fukuda and Nishimura 2002). In pansy (*Viola ×wittrockiana* Gams), increasing the percentage of FR light from 19% to 27% (or decreasing PPE from 0.77 to 0.72) by using a greenhouse spectral filter increased the peduncle length by 33% (Runkle and Heins 2003). In strawberries, the peduncle length determines the amount of space between the vegetative part of the plant and where the fruit is harvested (Darrow 1929). Many robotic harvesting prototypes for strawberries have reported peduncle detection as one of the major limiting factors for successful strawberry harvesting, a problem that would be remedied by consistent increases

Table 4. Individual fruit characteristics of strawberry 'Albion' and 'Monterey' plants grown under blue + red (B_{90} + R_{250}) or blue + red + far-red (B_{90} + R_{250} + FR_{50}) light-emitting diode lighting treatments.

Cultivar and treatment[i]	Fruit fresh mass (g)	Fruit diam (mm)	Fruit length (mm)	Total soluble solids (°Brix)
Albion				
B_{90} + R_{250}	10.8	27.1 a[ii]	31.1	6.9 a
B_{90} + R_{250} + FR_{50}	10.3	26.3 b	30.2	7.9 a
Significance	NS[iii]	*	NS	NS
Monterey				
B_{90} + R_{250}	11.2	27.4 a	30.7	7.7 b
B_{90} + R_{250} + FR_{50}	10.5	26.3 b	30.9	8.6 a
Significance	NS	*	NS	**

[i] Data represent the mean of two replications, with 12 plants per replication (n = 24).
[ii] Means followed by different letters within columns for each cultivar are significantly different by *t* test at $P < 0.05$.
[iii] NS, *, **Nonsignificant or significant at $P < 0.05$ or 0.01, respectively.

in peduncle length (Xiong et al. 2020). The increases in peduncle length using FR light in strawberries could prove useful for the successful application of machine harvesters to reduce labor costs, which can account for significant expenses in indoor vertical farms (Lubna et al. 2022).

Although the addition of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ FR light (or decreasing PPE from 0.88 to 0.84) did not affect flowering time in both long-day strawberry cultivars, it decreased the time to harvest the first fruit in 'Albion'. Also, in 'Albion', the addition of FR light increased the number of fruit, total fruit fresh mass, and the TSS content of fruit. Similar responses have been reported in tomatoes (Ji et al. 2020; Kim et al. 2020). When tomato plants received 50 to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light in addition to 150 to 170 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of combined B and R light, the additional FR light reduced fruit ripening time by 4 d, increased the dry mass of fruit by 33%, and increased the fructose and glucose content of ripened fruit by 32% and 42%, respectively (Ji et al. 2020). Increases of 50% in fresh yield, 26% in TSS content, and 77% in the dry mass of tomato fruit were also reported by Kim et al. (2020) by adding 95.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR light to 234 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of light provided by high-pressure sodium lamps, attributed to increases in dry mass partitioning to fruit and overall fruit sink strength. Fruit sink strength, a measure of the ability for plants to assimilate sugars and other organic compounds synthesized during photosynthesis into fruit, plays a pivotal role in the regulation of fruit development and ripening (Herbers and Sonnewald 1998; Marcelis 1996; Marcelis and Heuvelink 1999). Ji et al. (2020) observed that the additional FR light upregulated the genes responsible for fruit sugar transport and sugar metabolism, and increased dry mass partitioning to fruit, and the promotive effects of FR light on tomato fruit growth and quality were attributed to an increase in fruit sink strength. Increased fruit sink strength may also explain the increase in fruit yield, accelerated harvest, and improved quality of strawberry 'Albion' with FR light observed in our study.

Conclusion

For strawberry 'Monterey', leaf expansion was promoted with the additional FR light, which culminated in a parallel increase in shoot dry mass. Also, the addition of FR light extended the peduncle length in strawberry 'Monterey', suggesting a potential practical application of FR light to improve harvesting practices in indoor vertical farms, particularly for machine harvesters facing challenges in peduncle detection. In strawberry 'Albion', the addition of FR light had a minimal effect on vegetative growth, but increased fruit yield and TSS. In both 'Albion' and 'Monterey', FR light did not affect flowering time. Our findings indicate that the addition of FR light in sole-source lighting can increase vegetative growth, fruit yield, and quality in some long-day strawberry cultivars. However, further research on a wider range of cultivars is needed to comprehend more fully how the effects of adding FR light may differ across different strawberry cultivars.

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